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Original article

On the presence of the giant freshwater prawn, *Macrobrachium rosenbergii*, in French Guiana confirmed by citizen science and genetic analyses

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ABSTRACT

We report for the first time the presence of self-sustaining populations of *Macrobrachium rosenbergii* in French Guiana. Genetic analyses of the cytochrome *c* oxidase subunit I marker (COI) confirmed the identity of the species as well as historical records about the introduction of the species from commercial stocks. Despite the limited presence of *Macrobrachium rosenbergii* in French Guiana, the species is recorded in several river basins, including two where the species has never been farmed. This suggests that the species is able to disperse locally and highlights its potential invasive nature in the territory.

1. Introduction

Biological invasion is defined as the introduction of a species, voluntarily or not, in a region where it is not native and where its proliferation causes multiple damages to biodiversity. Due to globalization, the number of biological invasions has substantially increased in recent decades (Seebens et al., 2017), to the point where they are now considered one of the most important ecological disturbances threatening native biodiversity (Bellard et al., 2016; Vitousek et al., 1996). Invasive alien species can have multiple effects on biodiversity and ecosystem services, with numerous examples of impacts affecting natural environments (Kumschick et al., 2014; Witte et al., 1992), human health (Hulme, 2014; Jones et al., 2008; Ogden et al., 2019) and economic productivity (Bradshaw et al., 2016). In 2017 alone, the cost of biological invasions was estimated to be 163 billion USD (Diagne et al., 2021). Only a fraction of introduced species become invasive alien species. It is thus important to understand under which ecological conditions an introduced species might become invasive. In this context, we focus on the giant freshwater prawn *Macrobrachium rosenbergii*, a species widely introduced for aquaculture. The species has established feral populations in Dominica (Alston, 1991), Madagascar (Hanamura et al., 2008), Venezuela (Moreno et al., 2012), Brazil (Iketani et al., 2016; Oliveira and Santos, 2021) and Tanzania (Kuguru, 2019), raising concern about its invasive potential and impact on local fauna. In Brazil, the species has escaped from aquaculture farms and has long been registered in natural environments

(Barros and Silva, 1997; Cintra et al., 2003). Its current broad distribution suggests that it was also able to spread rapidly to new locations, highlighting its invasive nature (Cintra et al., 2003; Iketani et al., 2011; Oliveira and Santos, 2021; Silva-Oliveira et al., 2011).

Among the currently c. 200 species of freshwater prawns belonging to the genus *Macrobrachium* (Palaemonidae), the giant freshwater prawn, *M. rosenbergii*, is the biggest in the world (Ling, 1969; New, 2002), with males growing up to 330 mm in body length and weighing over 600 g. Two subspecies have long been suspected (sometimes referred to as “forms” or “races”), however, it is now well established based on genetic and morphological analyses that two species exist within its native range (de Bruyn et al., 2004a, 2004b; Wowor and Ng, 2007). *M. rosenbergii* sensu stricto (formerly known as *M. rosenbergii dacqueti*) is located West of the Huxley's line while *M. spinipes* (formerly known as *M. rosenbergii rosenbergii* and *M. wallacei*) is located East of the Huxley's line (Ng and Wowor, 2011 for details on the taxonomy; see Wowor and Ng, 2007, 2008). There are a number of biological and ecological characteristics that might explain its potential invasive nature. First of all, *M. rosenbergii* is characterized by a very high fecundity, with c. 80 000 eggs per female (the highest in the genus), compared to closely related species such as *M. amazonicum* with c. 2000 eggs per female (Da Silva et al., 2004). Its great size and agonistic behavior (Michael Bernard New et al., 2010) can also lead the species to outcompete native species. Finally, temperature has been shown to be the most important factor explaining the distribution of the feral populations in Brazil (Oliveira and Santos, 2021;

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Silva-Oliveira et al., 2011). The species can withstand a large range of temperature, reaching its highest growth between 24 and 31 °C (New, 2002), thus having potential to invade large areas in the Tropics (Silva-Oliveira et al., 2011).

The development of aquaculture for *M. rosenbergii* was made possible by a discovery in 1961 in Malaysia that found the species required brackish water to complete its reproductive cycle (Ling, 1969). In 1965, mass production techniques were developed in Hawaii with a broodstock introduced from Malaysia, which led to the commercial production of the species in 1972 (Fujimura, 1974). Since then, the giant freshwater prawn has been introduced in more than 40 countries and it has now become the most widely aquacultured freshwater prawn species in the world with a production representing 3% of the total crustacean global production (FAO, 2020; New, 2005). The introduction of *M. rosenbergii* in French Guiana, a French overseas territory of South America, can be directly traced to the original stock of the Fujimura lab in Hawaii, which was first introduced in Florida, then in Martinique, and finally in French Guiana (D. Lacroix pers. com.). Early tests were conducted in 1979–1980 to ensure that the species could indeed adapt to the local conditions. The first hatcheries were set up soon after and local production rose from 0.6 t in 1982 to 71 t in 1987 (Lacroix and Griessinger, 1988). The production then exceeded the consuming capacity of the local market which was estimated around 30 t. Despite success of the export market in 1989, commercialization was troubled by unreliable production, a lack of knowledge of the product by consumers in Europe and North America, and concurrent Asian production (Lacroix, 1991). In 1990, the State decided to halt its financial support, leading to closure of the hatchery and ultimately the end of giant prawn aquaculture in French Guiana (Lacroix, 2013).

Aquaculture of *M. rosenbergii* has been stopped in French Guiana for

30 years, and the species was considered absent from the territory. However, specimens were caught in the field in 2016 by the authors, suggesting that some populations may have persisted in the wild. The presence of the species indicates a potential risk of competition with local species as well as a risk of invasion to new environments. The main goal of the present study was to provide a first assessment of the presence of *M. rosenbergii* in French Guiana and to confirm the identity of the introduced species using a genetic analysis. Secondly, as recently performed for Brazil (Iketani et al., 2011), we aimed to retrace the introduction event(s) by comparing the local populations to the native populations using a barcoding analysis.

2. Materials and methods

2.1. Prospection and sampling

Because *M. rosenbergii* needs brackish water to complete its life cycle, prospection sites were located along the littoral band of French Guiana. 73 sites were sampled between 2019 and 2020 and positioned to cover the territory between East and West. At least one site was positioned on each stream where historical farming occurred (Fig. 1). To maximize the probability of detection of *M. rosenbergii*, sampling events occurred mostly during low water episodes: the dry season (August–December) and the “little summer of March” (March–April). Each site was sampled by one or two people walking on the banks for 1 h and a half at twilight when *M. rosenbergii* starts to be active. Specimens were detected with a powerful headlamp (1000 lumens) and collected with a handnet (2 cm mesh-size). Additionally, in some sites, active prospectations were completed by fitting three shrimp traps (de Farias Lima et al., 2016) on the banks overnight (6 p.m.–8 a.m.).

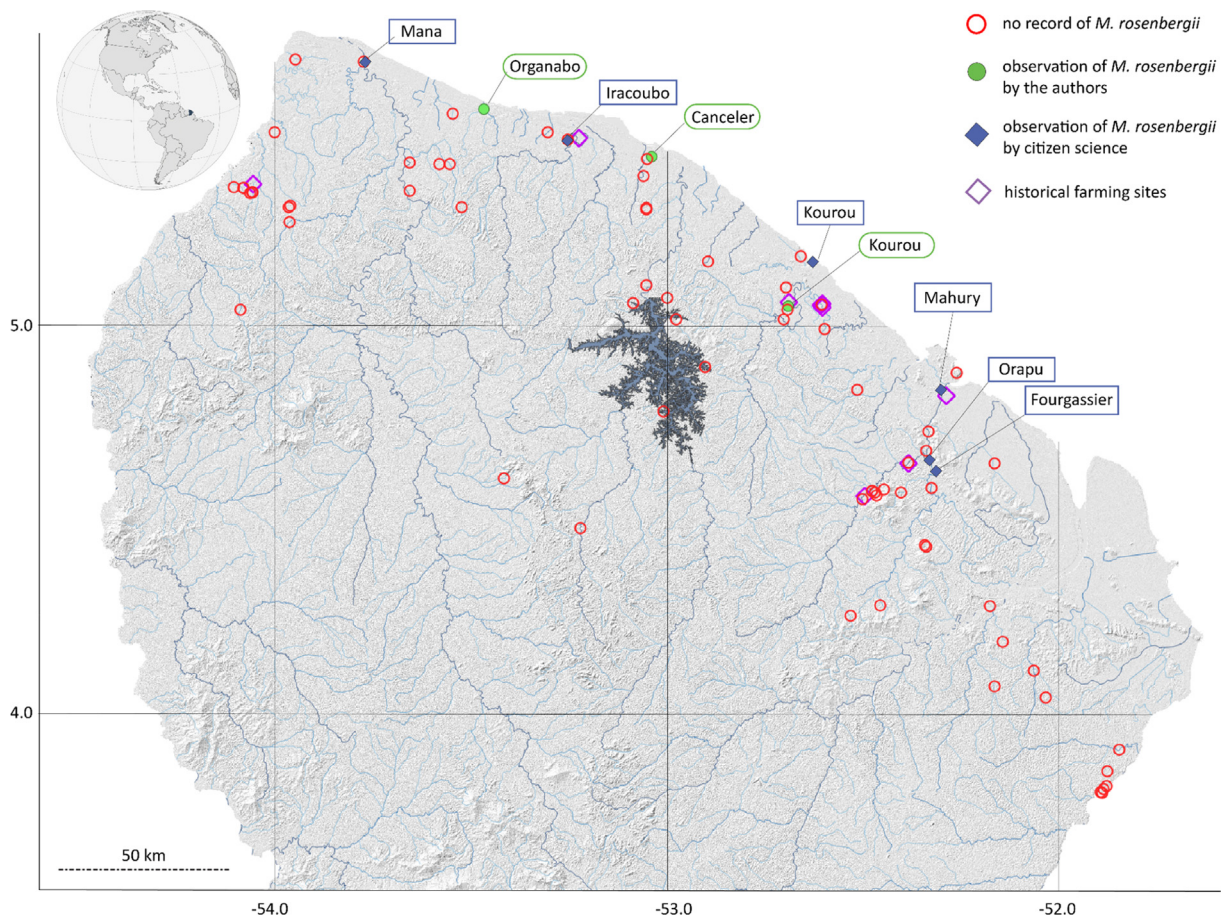


Fig. 1. Map of French Guiana presenting the historical farming sites as well as the prospected localities.

2.2. Citizen science

To complement the prospecting performed by the authors, we set up a citizen science program aimed at gathering information about potential observations of the species by local naturalists or fishermen. An information leaflet was distributed within various networks and a dedicated facebook page “Crevettes de Guyane” (@crevettedeguyane, 761 members) and email address (crevettesdeguyane@gmail.com) were set up. As naturalists in French Guiana tend to post pictures of unusual sighting on social media, we also investigated all major Facebook groups dealing with Nature in French Guiana, namely “LVG – Natures, Arts et Cultures de Guyane” (<https://fr-fr.facebook.com/groups/256075441400078>, 39,500 members), “Guyane Wild Fish Association” ([facebook.com/guyanewildfish](https://www.facebook.com/guyanewildfish), 13,000 members), “Détermination Faune Guyane” (<https://www.facebook.com/groups/305726770049351/>, 2600 members) and “Pêcheurs de Guyane” (<https://www.facebook.com/groups/1470374339866088>, 2500 members). For each group, we searched if members were mentioning the species or posting pictures.

2.3. DNA extraction, amplification and sequencing

Among the specimens collected by the authors, we selected 23 individuals from Crique Canceler, 16 from Crique Organabo, and 4 from river Kourou for downstream genetic analyses. Total DNA was extracted from one leg. After discarding the ethanol used for fixing specimens, samples were dried 15 min at 70 °C to ensure complete removal of the ethanol. We used the Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. Final elution was performed in 30 µL followed by a concentration of 5 min at 90 °C (final volume 15–20 µL). Purified genomic DNA was used as a template for PCR amplification. The standard 658 base pairs barcode of the mitochondrial protein encoding gene cytochrome c oxidase subunit I [COI hereafter] was amplified using the primer pair LCO1490 (5' GGT CAA CAA ATC ATA AAG ATA TTG G 3')/HCO2198 (5' TAA ACT TCA GGG TGA CCA AAA AAT CA 3') (Folmer et al., 1994) using the FastStart PCR Master (Roche, Mannheim, Germany). The total PCR volume was 25 µL and consisted of 2.5 µL of 10X reaction buffer, 2 µL of 10 mM dNTPs, 1.5 µL of 25 mM MgCl₂, 1 µL of each primer, 8.2 µL of H₂O, 0.2 µL of Taq Polymerase, and 10 µL of template DNA. The PCR cycles were as follows: 95 °C for 2 min, 35 cycles at 95 °C for 30 s, 50 °C for 30 s, and 72 °C for 1 min; and then a final extension at 72 °C for 7 min. The PCR products were verified by capillary migration on a QIAxcel Advanced system (Qiagen), and DNA quantitation was performed using PicoGreen (Turner BioSystems) on an Infinite F400 plate reader (Tecan). The purified PCR products were sequenced directly with the same primer pairs as used for amplification. The sequencing reactions were performed using BigDye Terminator ver. 3.1 (Applied Biosystems). The BigDye-labelled PCR products were purified using Sephadex G-50 medium (Sigma). The sequence reaction products were then analyzed using an ABI Prism 3730xl Genetic Analyzer (Applied Biosystems) by Genoscreen (Lille, France). Forward and reverse sequences were edited and assembled using Geneious (Kearse et al., 2012).

2.4. Data analyses

In order to test the identity of the French Guiana populations, we performed a phylogenetic analysis using several *Macrobrachium* species as outgroups, from which complete mitochondrial genomes had been sequenced for *M. nipponese* (Ma et al., 2011) and *M. lanchesteri*. We included reference sequences from native populations of *Macrobrachium rosenbergii* (de Bruyn et al., 2005) as well as *Macrobrachium spinipes* (de Bruyn et al., 2004a). Sequences were aligned in Muscle (Edgar, 2004) and the alignment was trimmed to the shortest sequence leading to a final alignment of 580 nucleotides. Tree search was performed using RAXML-ng (Kozlov and Stamatakis, 2019) starting from 10 random trees and 10 parsimony trees. Nodal support was estimated using Transfert Bootstrap Expectation (Lemoine et al., 2018) based on 1000 replicates and an

automated stopping procedure (Pattengale et al., 2010). Following Elsheikh et al. (2015), a Median-joining network was reconstructed from COI haplotypes of *Macrobrachium rosenbergii* from Malaysian populations, including the newly generated haplotypes from French Guiana.

3. Results

Of the 73 sites prospected, *Macrobrachium rosenbergii* was only detected in three sites. In two small rivers (Organabo and Canceler), up to 20 individuals were collected at night with a handnet, and in the Kourou river, between one and three individuals were collected on a regular basis using traps. Data gathered from the citizen science program offered complementary information. Indeed, in three rivers where we could not detect the species (Mana, Iracoubo and Mahury), reliable information through collection or pictures (Fig. 2) allowed us to record the presence of *M. rosenbergii*. Males and females, along with two development stages (eggs and juveniles) were observed.

We obtained barcode sequences for 43 individuals: 23 from Crique Canceler, 16 from Crique Organabo, and four from Kourou river. Those represent only two distinct haplotypes which are found in all localities where the individuals were found. The “majority haplotype” represent 78% of the samples in Crique Canceler, 94% in Crique Organabo, and 50% in Kourou river. The alignment used for the phylogenetic analysis comprised 81 sequences of 591 nucleotides with 67.2% identical sites and a mean pairwise identity of 91.3%. The phylogenetic analysis (Fig. 3) highlights that those two haplotypes form a monophyletic group with the remaining sequences belonging to the species *Macrobrachium rosenbergii*. The two haplotypes (Fig. 3) are identical to haplotypes found in Brazil (Iketani et al., 2011), but also to haplotypes from the native range (Malaysia, Bangladesh, Thailand, Vietnam) of the species (de Bruyn et al., 2005; Elsheikh et al., 2015).

4. Discussion

4.1. On the presence of established populations in French Guiana

The study of invasive species has recently received a renewed interest in French Guiana (Brosse et al., 2021). In this context, we provide the first evidence that the commercial species *Macrobrachium rosenbergii*, introduced and cultivated in French Guiana between 1982 and 1991 is present in natural conditions in several river basins over the territory. 30 years after farming stopped, specimens of *M. rosenbergii* were found by the authors in three locations (Kourou, Organabo and Canceler) and on three additional rivers (Mana, Iracoubo and Mahury) through citizen science. The presence of the species was confirmed by both prospecting and citizen science in only one site: the Kourou river. All development stages were observed, confirming the presence of self-sustaining populations. *M. rosenbergii* was collected by authors in great numbers and/or on a regular basis but only juveniles or small adults were collected (maximum length: 16 cm). Records of blue clawed males (Kuris et al., 1987) and ovigerous females (Fig. 2) were only obtained through citizen science in estuaries, an environment that was less prospected by the authors. The finding that most sites were close to historical farms is consistent with the notion of introductions from local farms rather than from aquarium trades (Padilla and Williams, 2004).

4.2. On the invasive potential of *M. rosenbergii*

The presence of *M. rosenbergii* seems to be limited in French Guiana. Of the 73 sites prospected by authors, only three revealed the presence of the species. However, this situation could be underestimated and result from sampling bias. Indeed, two of the rivers where *M. rosenbergii* was only found by citizen science (Mana and the affluents of the Mahury) had harbor sites which were intensely prospected by the authors during the last couple of years. This highlights the fact that even if the species is present, it might be difficult to collect specimens using traditional



Fig. 2. Observations of *Macrobrachium rosenbergii* by citizen science. Left panel: individuals collected on plage des roches, Kourou, by Olivier Marchal. Notice the ovigerous female. Right panel: blue clawed male collected in Mana by Rigdfort Raymond.

methods such as handnets and traps. Most of the citizen science observations were indeed obtained using cast-net fishing, trawling, or fishing rods.

The presence of *M. rosenbergii* on the Mana and Organabo rivers is particularly noticeable as there were never any aquaculture sites in the vicinity. We cannot rule out the possibility of an accidental or voluntary introduction of the species in those two sites, but it is most likely that the species was able to colonize new river basins by migrating from one estuary to the other through the coastal environment. The species is considered freshwater but requires brackish water to complete its life cycle and is known to present a wide tolerance to salinity with a median lethal salinity estimated at 24.6‰ (Chand et al., 2015). The coastal area of French Guiana is under the influence of the freshwater Amazon River plume which is brought along the Guianese coasts by the North Brazilian Current (Reul et al., 2014). It can thus harbor rather unsalted water (28–29‰) compared to the classical marine waters observed offshore (36–38‰). The mixing of the Amazon plume with oceanic waters is a complex system but under certain discharge and current conditions, coastal waters have been measured at 17‰ 50 km off the coast of French Guiana (Lambs et al., 2007), rendering a coastal migration of *M. rosenbergii* plausible. This highlights the necessity of including estuaries in surveillance programs moving forward. Based on the unified framework for biological invasions proposed by Blackburn et al. (2011), we consider that the species should be classified under the category D2 “self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction”. This is the last stage before the species can be considered fully invasive (category E).

It is important to note that the presence of the North Brazil Current, a strong littoral current oriented East-West on the guyanese littoral (Chevalier et al., 2004), could limit the implantation of the species. Because the planktonic larvae are not good swimmers, colonization of basins situated in the East (against the current), is unlikely to occur. The absence of observations in river basins situated East of past aquaculture sites could be linked to this situation. However, it is important to remain careful about the absence of the species in the East of French Guiana as the absence of observation data could be linked to the above-mentioned low detectability of the species. The presence of *Macrobrachium carcinus*, a potential local competitor, could also curb the invasion of *M. rosenbergii*

in French Guiana. Both species need brackish water to complete their life cycle. *M. carcinus* is slightly smaller than *M. rosenbergii*, with the biggest individuals reaching 30 cm (Holthuis, 1952). Despite intensive searches by the authors in the Comté river where the biggest farms occurred, no individuals of *M. rosenbergii* were collected while only one or two individuals of *M. carcinus* were present. On the other hand, in the rivers where *M. rosenbergii* were abundant (e.g. Organabo and Canceler) or regularly collected (Kourou river), no individuals of *M. carcinus* were detected.

4.3. On the origin of the Guyanese populations

In order to trace the geographic origin of the populations found in French Guiana, we compared our sequences to the haplotypes found in Brazil (Iketani et al., 2011) as well as in the native range of the species (de Bruyn et al., 2005; Elsheikh et al., 2015). Interestingly, we found that the two French Guiana haplotypes are also present in Brazil (referred to as “haplotype 12” and “haplotype 34”; Iketani et al., 2011). Haplotype 12 is also found in native populations of Bangladesh and Thailand while haplotype 34 is found in native populations from Vietnam (de Bruyn et al., 2005). Considering the level of genetic distance between the two haplotypes, Iketani et al. (2011) concluded that the Brazilian populations originated from distinct introductions from Vietnam and either Bangladesh or Thailand. However, this conclusion is based on very few samples from Malaysia in the de Bruyn et al. (2005) dataset, the original source of the commercial stock. Since then, additional sequences from the native range of the species in Malaysia have been provided (Elsheikh et al., 2015), which allow us to reach different conclusions. When comparing the French Guiana/Brazilian haplotypes with sequences from native populations from Malaysia (Fig. 3), we find they share 100% similarity with Malaysian haplotypes (namely KM234160 and KM234139, KM234146, KM234166). Our analysis thus confirms the historical records that populations found in French Guiana and Brazil are most likely related to an introduction event from the commercial stock of *M. rosenbergii*, itself originating from Malaysian specimens.

4.4. Perspectives

Invasive alien species can impact local fauna through multiple

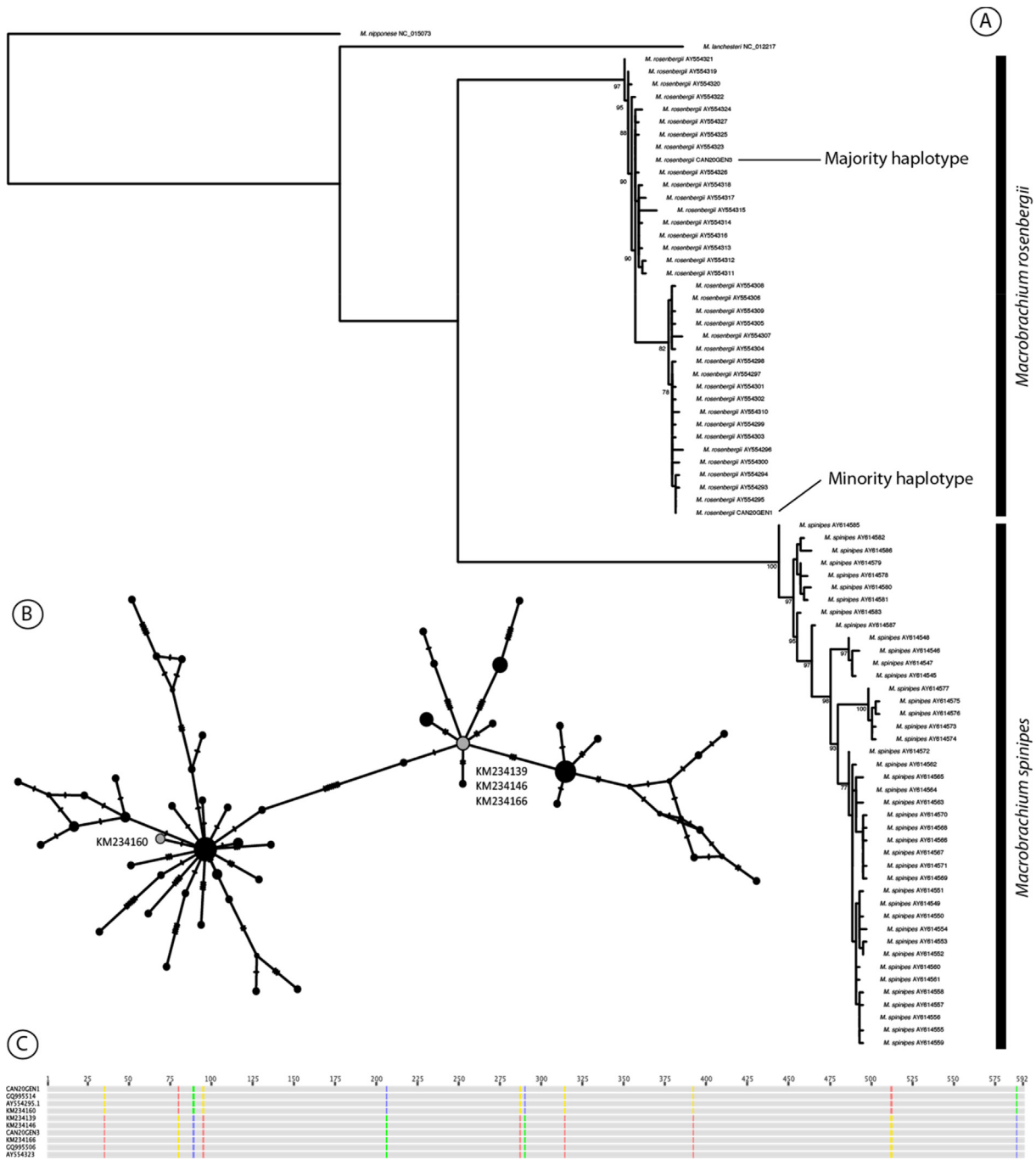


Fig. 3. A Maximum Likelihood phylogenetic tree of the COI gene inferred using RAxML-ng and a GTR + G model. Nodal support on nodes represents Transfer Bootstrap Expectation values. Data from *M. rosenbergii* native range are from de Bruyn et al. (2005) while data from *M. spinipes* native range are from de Bruyn et al. (2004). B Median-joining network reconstructed from COI haplotypes of *Macrobrachium rosenbergii* from Malaysian populations, inferred from Elsheikh et al. (2015) dataset. Grey haplotypes represent the ones identical to the “Majority” and “Minority” haplotypes found in French Guiana. C sequences of the haplotypes found in French Guiana and their counterparts in the datasets of de Bruyn et al. (2005), Iketani et al. (2011) and Elsheikh et al. (2015).

mechanisms including predation, competition, hybridization, or spread of diseases (Bruno et al., 2005; Mack et al., 2000; Ruiz et al., 1997; Vitousek et al., 1996). To date, no adverse ecological impacts have been reported and *M. rosenbergii* is generally considered harmless (Anger, 2013). For example, in Dominica, the species only established in areas where native shrimp had been eliminated (Alston, 1991). In addition, the risk of hybridization with native species is considered low (Graziani et al., 2003). However, informal records suggest that the species might be outcompeting native shrimps and also affecting fish communities (Williams et al., 2001), especially in equatorial regions harboring ecological characteristics similar to the native range of the species. In French

Guiana, it is thus important to (i) provide an assessment of the local native fauna and (ii) carefully investigate the impact of the introduction of *M. rosenbergii* on native species. In addition, detection of the species has proven difficult using classical sampling methods. Alternative approaches based on environmental DNA could be evaluated for the development of a monitoring program in French Guiana.

5. Conclusion

Here, we provide for the first-time evidence that the commercial species *Macrobrachium rosenbergii*, introduced and cultivated in French

Guiana between 1982 and 1991 is present in natural conditions in several river basins throughout the territory. The presence of populations in basins where the species was never cultivated suggests that the species was able to colonize new locations, highlighting its potential invasive nature. Our molecular analyses confirmed the identity of the species as *M. rosenbergii* and showed the presence of two haplotypes in the territory. It also confirmed historical records that the populations found in French Guiana were derived from an introduction of the commercial stock.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Jérôme Muriene: Conceptualization, Methodology, Formal analysis, Writing - original draft. Johan Chevalier: Funding acquisition, Conceptualization, Investigation, Validation, Writing - reviewing and editing. Simon Clavier: Funding acquisition, Conceptualization, Investigation, Validation, Writing - reviewing and editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.watbs.2022.100039>.

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